

Review

Integrating biological control as a sustainable approach for managing silver scurf and black dot in potatoes

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HIGHLIGHTS

- Black dot and silver scurf are widespread tuber blemish diseases causing major postharvest losses.
- Existing management tools for management of potato tuber blemish diseases are effective to some extent but insufficient alone.
- Biocontrol agents have shown strong *in vitro* activities but lacks field validation.
- Combining biologicals with other management strategies could offer a sustainable tuber disease management strategy.

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ABSTRACT

The potato (*Solanum tuberosum*) is a globally cultivated crop, but blemish diseases such as silver scurf (*Helminthosporium solani*) and black dot (*Colletotrichum coccodes*) cause significant quality and market losses, black dot could reduce yield up to 30–50 % with estimated market loss of ~ £3 million yearly and silver scurf can cause tuber weight losses up to ~ 17 %. The origins of these diseases are multifaceted, involving complex interactions among pathogens, environmental conditions, and the host plant. This review aims to offer a thorough examination of current knowledge on their biology, epidemiology, and management practices, highlighting that cultural practices such as crop rotation, reduced tillage, regulated irrigation, curing and controlled storage conditions reduce disease severity, but are insufficient as standalone management strategies. Numerous bacterial and fungal biocontrol agents have shown strong *in vitro* inhibition but still require field validation. Plant derived metabolites and microbial metabolites also exhibited potent antifungal activity against these diseases under *in vitro* dual culture assays, mini-tuber assays and as post-harvest protectants. Although combining biocontrol agents with early detection, optimized agricultural practices, and regulated storage conditions has not yet been fully validated for potato tuber blemish diseases, similar integrated pest management strategies have proven successful against other crop diseases, highlighting the potential of this approach but also signifying the need for further research. Thus, this review highlights the existing biological management approaches investigated against black dot and silver scurf and the possibility of incorporating it with other non-chemical approaches for sustainable management of these diseases.

1. Introduction

Potato (*Solanum tuberosum*) is the fourth most important food crop worldwide, after rice, wheat, and maize, and is cultivated in more than 150 countries, serving as a major dietary food in both developed and developing regions (Food and Agriculture Organization, 2025). As tubers are the valuable part of the potato plant, soilborne and tuber borne

diseases become a cause for substantial concern (Massana-Codina et al., 2021). Soilborne diseases affecting potato crops can be broadly classified into two, those that impair vegetative growth and those that primarily reduce tuber quality. The first group includes diseases late blight (*Phytophthora infestans*), bacterial wilt (*Ralstonia solanacearum*), leaf spot (*Alternaria alternata*), early blight (*Alternaria solani*), and viral diseases (e.g., Potato virus Y, Potato leafroll virus). The second group consists of

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galls, blemishes, and rots (Gudmestad et al., 2007). Among these, blemishes such as black dot (*Colletotrichum coccodes*), black scurf (*Rhizoctonia solani*), silver scurf (*Helminthosporium solani*), common scab (*Streptomyces scabies*), and powdery scab (*Spongospora subterranea*) contribute major loss in market value, often displayed as varying degrees of scabby or tuber skin perturbations (Hide et al., 1994a).

With global distribution and economic impact, black dot and silver scurf hold substantial importance in potato production (Massana-Codina et al., 2021). Currently, over 90 % of potatoes intended for the fresh market are washed, making consumers more sensitive to even minor external defects, which has magnified the economic consequences of these two diseases (Keiser et al., 2012). Various methods such as crop rotation, early harvesting and shorter storage periods, have been implemented to address the non-chemical management of these diseases, but their effectiveness remains limited and insufficient alone (Tiwari et al., 2021). The application of fungicides such as tolclofos-methyl, dichlorophen, thiabendazole, and azoxystrobin have been shown to significantly reduce the impact of these diseases, but growing concerns remain regarding their negative effects on consumer health and the environment, as well as on the emergence of fungicide-resistant isolates (Andrivon et al., 1997; Tsror and Peretz-Alon, 2004). For instance, *H. solani* isolates that are resistant to thiabendazole, azoxystrobin and thiophanate-methyl have been reported (Chudinova et al., 2020; Puri et al., 2025).

Given the challenges with fungicides, the demand for organic potatoes is increasing due to avoidance of chemical usage in its production compared to conventionally grown potatoes (Rembiałkowska, 2007). This trend is reinforced by the rise in organic agriculture, with certified organic farmland reaching ~ 240 million acres in 2022, that is more than five-fold increase since 2000 (Rasmussen et al., 2024). However, the major challenge encountered by the organic potato producers in managing tuber blemish disease like silver scurf and black dot were the unavailability of effective non-chemical management strategies (Mattupalli et al., 2013). However, the use of inorganic salt-based treatments, including sodium bicarbonate and sodium carbonate, are permitted in organic farming in many jurisdictions (USDA NOP, EU organic standards, Canada Organic Standards) have proved successful in managing silver scurf under commercial potato storage conditions. Nevertheless, sodium carbonate caused slight periderm discoloration at 0.2 M, and both salts showed inconsistent lesion suppression across experiments, with sodium bicarbonate in particular providing variable efficacy (Olivier et al., 1998). Furthermore, no potato varieties exhibiting complete resistance to these diseases have been discovered (Massana-Codina, 2020).

Biological control (biocontrol) of plant diseases refers to the use of living organisms to suppress the growth, activity, or survival of phytopathogens on their host plants (Collinge et al., 2022). The key advantages for biocontrol approaches include establishing a beneficial microbial community in the rhizosphere, enhancing overall host plant health, promoting growth, increasing nutrient availability and fortifying host resistance against both biotic and abiotic stresses (Ayaz et al., 2023). Beneficial biocontrol agents have shown to suppress pathogens either directly by outcompeting them for space and nutrients (competition), invading the pathogen (hyperparasitism), producing antimicrobial compounds (antibiosis) or indirectly by activating the plant's own defense mechanisms (induced resistance) (Montoya-Martínez et al., 2024). Recent findings also suggest that biocontrol agents could interfere with pathogen quorum sensing and can also attract and reshape the soil microbiota to defend against pathogens (Zhang et al., 2023). Beneficial microbes can have specific advantages over synthetic fungicides in having fewer non-target and environmental impacts and efficacy against fungicide resistant pathogens (Asad, 2022). Some biocontrol strategies, such as *Trichoderma*, *Bacillus* and *Pseudomonas* based products have already been incorporated into commercial bioformulations (Khan et al., 2023). So, implementation of sustainable biocontrol based environmentally friendly methods applicable to both

conventional and organic potato production for the effective management of black dot and silver scurf may be a future perspective. This review aims to consolidate current knowledge on the pathogens responsible for black dot and silver scurf, critically assess the effectiveness of existing biological management strategies, and propose potential strategies to enhance sustainable disease control practices by integrating biocontrol with other non-chemical existing strategies at appropriate stages of potato production.

2. The pathogens – *Colletotrichum coccodes* (Wallr.) S. Hughes and *Helminthosporium solani* Durieu and Montagne

2.1. Symptoms and pathogen biology

The black dot of potatoes is caused by *Colletotrichum coccodes* (*C. coccodes*), an ascomycetous fungus belonging to the family Glomerellaceae in the order Glomerellales and class Sordariomycetes (Hughes, 1958). Typical symptoms of black dot are irregularly margined clusters of black dots (microsclerotia/acervuli) on tubers, stolon and aerial parts of the potato plant (Fig. 1a-c) (Hunger and McIntyre, 1979a). Microsclerotia serves as dormant survival structures composed of thick melanized hyphae, providing protection during overwintering and exposure to abiotic and biotic stresses (Andrivon et al., 1997). Remarkably, microsclerotia can endure extended periods in the soil, persisting for up to 13 years (Cullen et al., 2002). The viability rates for microsclerotia were further supported by a field investigation, that demonstrated a survival rate of 92 % in tomato cultivated soil for a prolonged period of eight years (Dillard and Cobb, 1998). It has also been found that *C. coccodes* produces asexual fruiting bodies called acervuli (approximately 200–300 µm in diameter) to disseminate septate and branched conidiophores with 10–20 µm long and 3–4 µm wide fusiform conidia (Fig. 1d) (McIntyre and Rusanowski, 1975).

Silver scurf is caused by the ascomycete fungus *Helminthosporium solani* (*H. solani*), classified under subphylum Pezizomycotina, class Dothideomycetes, subclass Pleosporomycetidae, order Pleosporales, and family Pleosporaceae (Wallroth, 1833). Symptoms of silver scurf include silvery patches with well-defined dark brown margins exclusively on the potato tuber surface (Fig. 1e-f) (Hunger and McIntyre, 1979). *H. solani* produce conidiophores with conidia as a means of dissemination (Fig. 1g-h). The conidiophores arise from the stromata bearing multicellular (two to eight pseudosepta which arise in whorls of conidiophores), large, club-shaped and pale to dark brown conidia produced in a basipetal succession (Errampalli et al., 2001; Luttrell, 1964). The non availability of the hard survival structures substantiate the inability of *H. solani* spores to thrive viable long in soil. The fungal mycelia of both the pathogens are white with evenly distributed grey to black conidia on artificial media (Fig. 1i-j).

2.2. Host range

The host range of the *C. coccodes* was found to be rather broad in various plants and weeds with frequent infections observed in plants belonging to families Solanaceae, Cucurbitaceae, Apiaceae, Liliaceae, Chenopodiaceae, Brassicaceae, Asteraceae and Fabaceae (Mikulic-Petkovsek et al., 2013; Rodriguez-Salamanca et al., 2012). On the other hand, the host range of *H. solani* is restricted only to the potato plant (Frazier et al., 1914). However, asymptomatic colonization of the *H. solani* has been observed in the senescent leaf tissues of crops such as alfalfa, corn, wheat, and rapeseed (Mérida and Loria, 1994). This saprophytic ability concerns the need to reconsider the impact of these host species on the silver scurf disease cycle.

2.3. Disease cycle

The infection cycle and growth conditions of both the pathogens are almost similar in terms of inoculum, spread and influencing

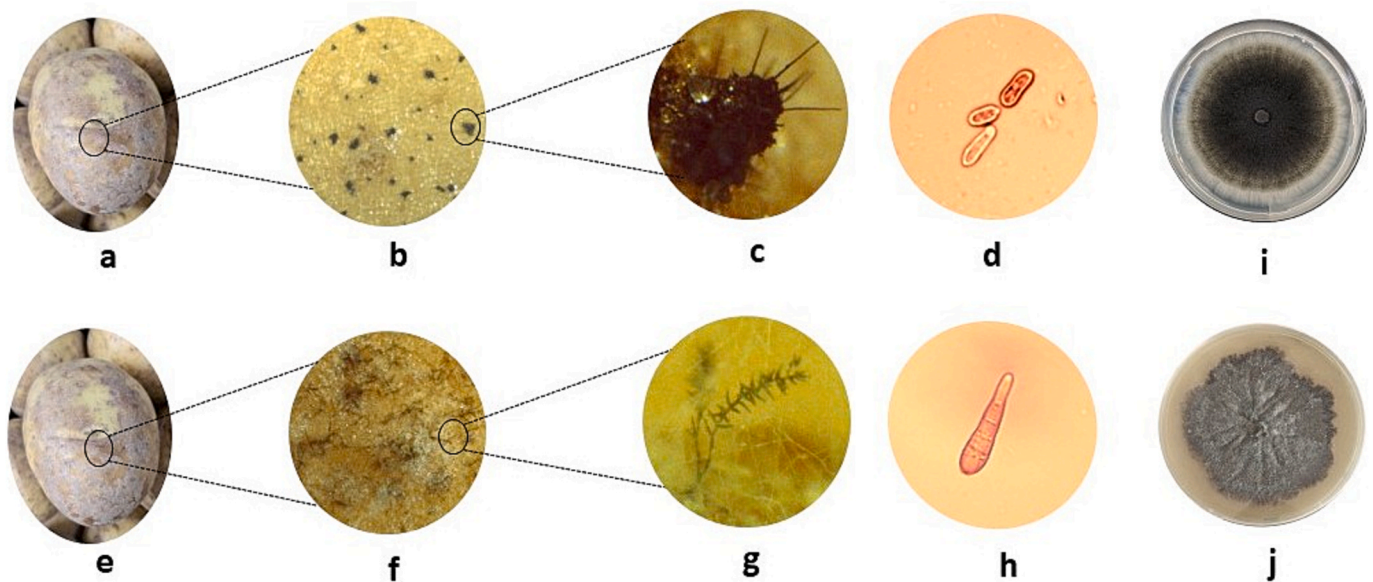


Fig. 1. Symptoms and morphological features of *C. coccodes* and *H. solani*. (a) Black dot lesions on tuber surface; (b) Magnified view of *C. coccodes* microsclerotia and acervuli on tuber surface; (c) *C. coccodes* acervuli bearing setae and conidiophore with conidia; (d) Conidia of *C. coccodes* (Scale bar = 6 µm); (e) Potato tuber with silver scurf lesions; (f) Magnified view of *H. solani* conidiophore on tuber surface; (g) *H. solani* conidiophore bearing conidia; (h) Conidia of *H. solani*; (i) *C. coccodes* growing on PDA media; (j) *H. solani* growing on V8 media.

environmental conditions. The primary inoculum of the infections is from infected tuber (Fig. 2a and Fig. 3a) or soil debris with conidial spores or hyphae overwintering as microsclerotia (*C. coccodes*) or mycelia (*H. solani*), which usually occur during the initial days of planting (Fig. 3b) during the spring (Massana-Codina, 2020).

Comparative observations on source of inoculum indicate that the disease incidence occurs prominently through soil in the case of black dot and infected tuber for silver scurf (Jellis and Taylor, 1977; Nitzan et al., 2008). During the spring, warm soil temperatures within the range of 15–25 °C, along with high soil moisture resulting from frequent rainfall or poor drainage, create ideal conditions for the initiation of black dot and silver scurf infections at the root system (Figs. 2b, 3c) (Massana-Codina et al., 2021). From there, the *C. coccodes* infection spreads to stolons, stems, and progeny tubers, with symptoms emerging around fall when plants enter the tuber bulking stage with foliage beginning to senesce (Nitzan et al., 2006). Meanwhile, *H. solani* continues its colonization within the stolon base and newly formed tubers (Andrison et al., 1997). Symptoms like chlorosis, necrosis, dark purple coloration on inner surface of root or the appearance of black dot microsclerotia become apparent when plants experience stress or begin senescing near harvest time (Fig. 2c). Towards the end of the season, microsclerotia become visibly apparent on roots, stolons, and stems (Fig. 2d) (Nitzan et al., 2008, 2006). Secondary infections of *C. coccodes* typically establish during summer through conidia, often disseminated by wind, rain or irrigation thus exhibiting a polycyclic mode of lifecycle during the growth season (Fig. 2e–i) (Lees et al., 2010). Disease symptoms of *H. solani* are usually unnoticed until harvest as they do not manifest on the haulm or roots and are restricted to the tuber periderm where it follows a monocyclic lifecycle (Figs. 3d,e) (Fahn, 1982). In both diseases, tubers can become infected in the field without displaying obvious lesions until they are stored (Fig. 2j–k, Figs. 3h–i) (Nitzan et al., 2006). *C. coccodes* manifest as dark, deep sunken black dots on potato tubers without clear margin, while *H. solani* causes silvery lesions with distinct margins that merge as the disease advances during prolonged storage temperatures between 5 and 15 °C (Glais-Varlet et al., 2004). On extended periods of storage, these blemishes deepen the permeability of the tuber skin through minor cracks, resulting in weight loss and shrinkage (Heiny and McIntyre, 1983; Jellis and Taylor, 1977). The dispersion of conidia through the ventilation system can also be a means

of secondary infections in other healthy tubers in potato storage facilities where multiple infections can take place within and between the tubers (Figs. 2k,3i) (Tiwari et al., 2021). Sporulation of these pathogens can increase after washing and packaging of potatoes for consumption leading to deteriorating quality (Figs. 2l,3j) (Errampalli et al., 2001). Epidemiological insights showed that minimum temperature and humidity conditions for the development of infection for both the fungi are 3 °C and 90 % relative humidity with optimum growth at warm temperatures of 15–21 °C and high humidity of 95 % (Hunger and McIntyre, 1979). Visual assessment alone could only manifest extreme cases of infection as validated in field trials and controlled environment experiments, whereas asymptomatic seed tubers could also yield diseased progeny tubers (Massana-Codina et al., 2021). The limitations of visual assessments in disease detection necessitates the need for implementing advanced detection methods for more accurate early pathogen detection strategies and management of these blemish diseases (Lees et al., 2010; Read and Hide, 1988).

3. Global distribution of black dot and silver scurf

The black dot disease in potatoes has historical origins dating back to 1833 in Germany and silver scurf was first documented in Moscow in 1871 (Hars, 1871; Wallroth, 1833). The diseases were considered common, but not a significant concern for potato productivity till early 19th and 20th century, while it gained global recognition in the late 20th Century when the outbreak significantly impacted the potato industry, especially the fresh market and chip-making sector with a market loss of £ 3 million in UK and 20–40 % loss in Colorado (Hide et al., 1994b; Hunger and McIntyre, 1979a). Consumer demand for visually appealing, high-quality potatoes increased concerns about aesthetic issues such as pigmentation loss in red skinned tubers, appearance of irregular patches, and shrinkage of tubers resulting in depreciation of their market value (Jiang et al., 2022). The global spread and incidence of these diseases have been a major concern over the years, evident from reports spanning from the 20th century to recent observations around the world (Table 1). This underscores the need for timely disease surveillance and effective management practices to address emerging threats around the world.

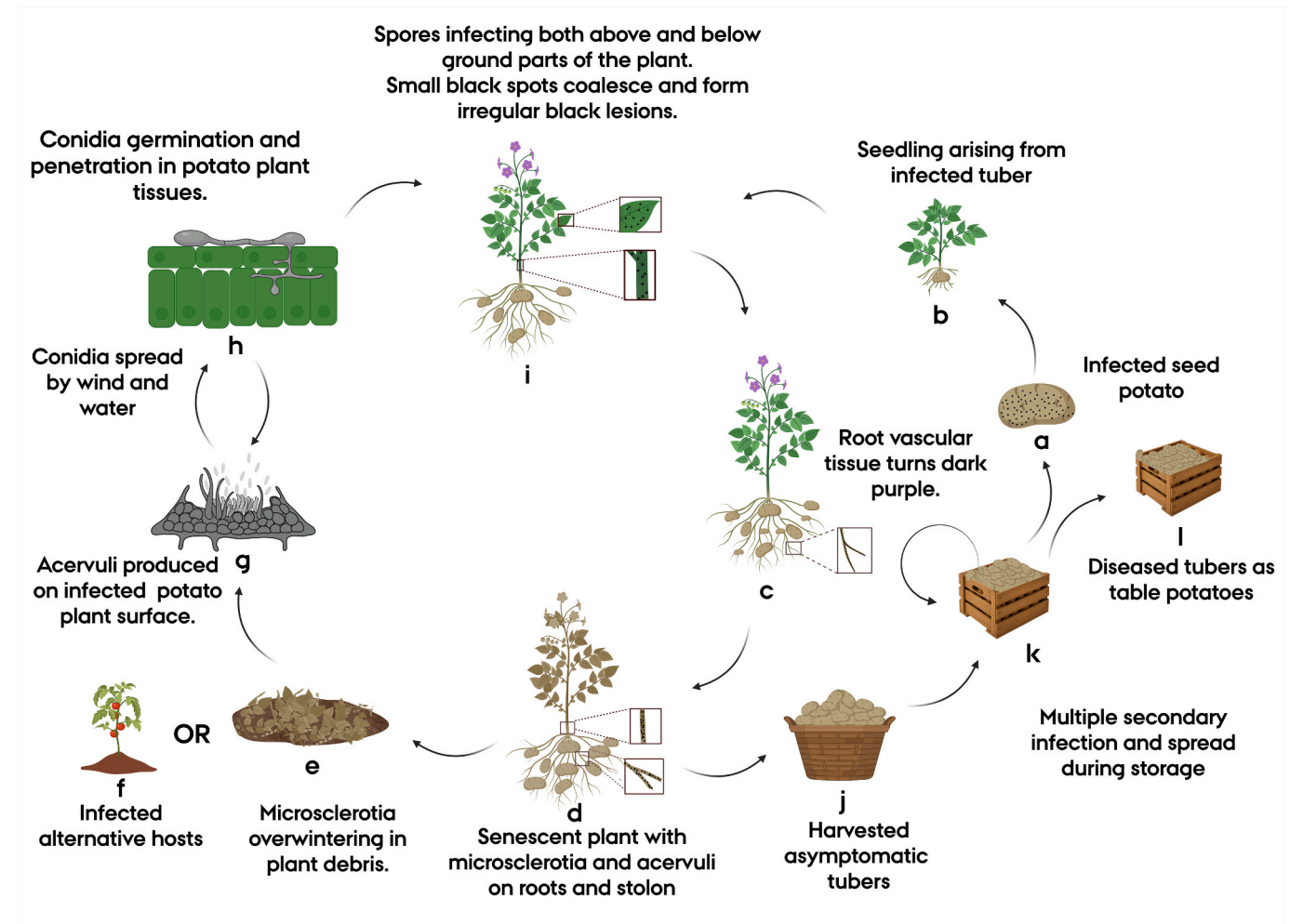


Fig. 2. Disease cycle of *C. coccodes*. (a) Infected potato seed tuber from storage; (b) Seedling arising from infected tuber; (c) Magnified image showing root vascular colonization of *C. coccodes*; (d) Plant senescence and *C. coccodes* spread on underground tubers; (e) Plant debris with overwintering microsclerotia; (f) Alternative host; (g) Acervuli releasing conidia; (h) Disseminated conidia causing secondary infections on tissues of new plants; (i) Mature plant with infection; (j) Harvested asymptomatic tubers; (k) Secondary infection during storage and symptom development; (l) Table potatoes with symptoms all over. This figure was created with BioRender (<https://biorender.com/gvyyryx>).

4. Currently employed non-chemical management strategies

The prevailing methods utilized to manage black dot and silver scurf is predominantly linked to cultural and chemical interventions (Andrison et al., 1997; Johnson and Cummings, 2015; Tsror and Peretz-Alon, 2004). Chemical methods like the use of thiabendazole and azoxystrobin could suppress infections of black dot and silver scurf, but their excessive use can have a negative impact on the environment and result in the emergence of resistant pathogen strains that compromise disease control (Andrison et al., 1997; Djaman et al., 2021; Tsror and Peretz-Alon, 2004). Various cultural practices in potato cultivation such as planting of clean seed tubers, planting and harvest timing, irrigation, curing and crop rotation are known to influence the development of these diseases (Errampalli et al., 2001).

Planting of disease free tubers has been reported to have a negative correlation with the incidence and severity of these diseases (Geary and Johnson, 2006; Lees et al., 2010). Moreover, crop rotation has been reported to be effective at reducing incidence of silver scurf and black dot. An interval of five or more years between subsequent potato cultivation has been found to significantly reduce the incidence of black dot in commercial fields (Johnson and Cummings, 2015). Since *H. solani* does not survive in field soil for more than a year, silver scurf is seldom observed on tubers from fields where crop rotations extend beyond three

years (Mérída and Loria, 1994). Short crop rotation with potatoes had little effect on the black dot incidence, while its severity was significantly lowered in fields that had not been used for potato cultivation for seven years (Hide and Read, 1991). It is worth noticing that rotating the field with crops like barley, maize, rye, wheat, and orchard grass showed significant reduction in the blemish infection rates in the subsequent season of potato production (Nitzan et al., 2006). Additionally, the cultivation of high glucosinolate (high-GSL) mustard improved the management of silver scurf with a significant severity reduction level of 28–60 % compared to other rotational crops like rapeseed and canola (Larkin and Lynch, 2018).

Thus a long-term crop rotation between potato harvests of 5 to 7 years for *C. coccodes* and 2 to 3 years for *H. solani* with incompatible rotational crops can significantly decrease the likelihood of these blemishes (Emmond and Ledingham, 2011; Johnson and Cummings, 2015). Planting density is another key factor influencing the severity of these diseases. Higher tuber density leads to an increased number of progeny tubers, and potato plants with shorter stolon that exacerbate disease severity by causing more tubers to come into direct contact with each other (Firman and Allen, 1995). The incorporation of reduced tillage (without ploughing but using spring-tine cultivator) and a 3-year crop rotation with spring barley and clover significantly reduced the severity of silver scurf and black dot, and also improved soil structure,

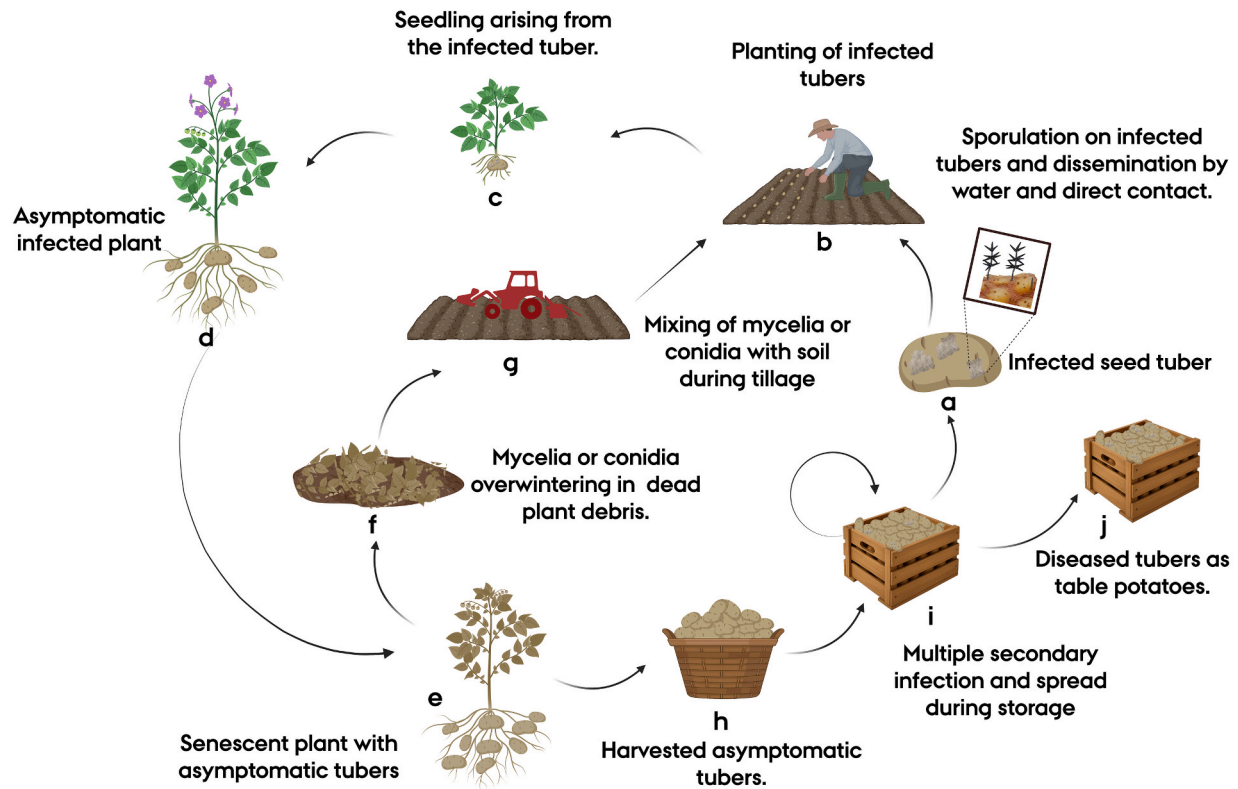


Fig. 3. Disease cycle of *H. solani*. (a) Infected potato seed tuber with conidiophore ready to disseminate conidia; (b) Planting of infected tubers; c. Plantlet arising from infected tuber; (d) Mature plant with infection; (e) Plant senescence; (f) Plant debris with overwintering mycelia; (g) Mixing of mycelia/ conidia with soil during tillage; (h) Harvested asymptomatic tubers; (i) Secondary infection during storage and symptom development; (j) Table potatoes with symptoms all over. This figure was created in BioRender (<https://BioRender.com/sok5hto>).

enhancing soil conservation and reduced fertilizer inputs (Peters et al., 2004). During the growing season, the increase in the rate of irrigation could increase the severity of the black dot, while it has a negative correlation with the severity of silver scurf (Adams et al., 1987). On the other hand, silver scurf incidence was higher on uncured potatoes that received irrigation shortly before harvest (Hide et al., 1994b). Therefore, irrigation except under drought conditions and avoidance of watering just before harvest could be an effective strategy to reduce the severity of black dot and silver scurf. Research findings indicate that early planting and early harvest could also significantly reduce the severity of black dot and silver scurf disease, particularly when there is a high amount of the pathogen present in the soil (Brierley et al., 2015). A two-hour windrowing (loosening and partially drying harvested potato tubers by mechanically lifting them from the soil and arranging them in long, narrow rows on the soil surface) followed by curing reduced silver scurf, though other studies found its effects during storage to be limited and inconsistent (Firman and Allen, 1995; Hide et al., 1994b).

As black dot and silver scurf are considered post-harvest diseases proper post-harvest management is crucial for minimizing the severity of these diseases. For instance, dry curing of potatoes at low relative humidity of 80–85 % has reduced the development of these diseases (Frazier et al., 1998; Peters et al., 2016).

Even though these approaches are already adopted in organic and conventional potato production systems, silver scurf and black dot are still a problem of concern in potato market, so combining the use of biological control along with the existing cultural practices could potentially offer an effective strategy to control silver scurf and black dot in organic potato production systems.

5. Biological management of black dot and silver scurf

Various biocontrol strategies, including the use of living antagonistic microbes, plant and microbe derived metabolites, bio-protectants (non-volatile secondary metabolites, volatile organic compounds (VOCs) derived from plants or microbes), and commercially approved biocontrol formulations (Fig. 4), have demonstrated strong inhibition of *C. coccodes* and *H. solani* with 30–70 % symptom reduction under greenhouse and small scale storage trials and up to 90–100 % of growth and spore germination under laboratory conditions (Khan et al., 2020; Steglińska et al., 2022c; Wei et al., 2023). Despite strong research evidence for pathogen suppression and reduced lesion development, commercial adoption of biocontrol agents remains limited due to inconsistent field performance, formulation stability issues, regulatory barriers, higher costs, and limited farmer awareness (Kmocho et al., 2023). Bridging this gap requires product optimization, large-scale validation in field and effective extension efforts.

5.1. Living microbes as biocontrol agents against black dot and silver scurf

5.1.1. Bacterial biocontrol agents

A wide variety of bacterial genera including *Bacillus*, *Xanthomonas*, *Streptomyces*, *Pseudomonas* etc. have been used to control black dot and silver scurf diseases (Elson et al., 2007; Lysøe et al., 2017; Martinez et al., 2002; Michaud et al., 2007). For instance, bacteria from silver scurf disease suppressive soils such as *Nocardia globerula*, *Pseudomonas putida*, *Cellulomonas fimi*, *Rhodococcus erythropolis*, *Kocuria varians*, *Pseudomonas fluorescens*, *Aquaspirillum autotrophicum*, *Bacillus mycoides*, *Clonostachys rosea*, *Kocuria rosea* and *Streptomyces griseus* exhibited over 50 % inhibition of *H. solani* conidiophore development on tuber surface,

Table 1
Reports on global impact of black dot and silver scurf across the world.

Country / Region	Pathogen	Incidence / Severity	Data Type	Reference
Australia	<i>C. coccodes</i>	Presence reported	Field survey	(Chang, 2024)
Bulgaria	<i>C. coccodes</i>	Presence reported	Field survey	(Manova et al., 2022)
Chile	<i>C. coccodes</i>	Presence reported	Field survey	(Alananbeh et al., 2024)
China (Tibet)	<i>C. coccodes</i>	Presence reported	Field survey	(Zhong et al., 2022)
China	<i>H. solani</i>	10 % tubers infected	Field survey	(Tian et al., 2007)
Denmark; France; Netherlands	<i>C. coccodes</i>	66 % seed-tuber lots infected	Seed tuber survey	(Abu-El-Samen and Al-Bdour, 2011)
Denmark, France, Netherlands	<i>H. solani</i>	93 % seed-tuber lots infected	Seed tuber survey	(Abu-El-Samen and Al-Bdour, 2011)
Egypt	<i>C. coccodes</i>	Presence reported	Greenhouse pathogenicity test	(El-Marzoky, 2013)
Europe	<i>H. solani</i>	96 % of lots infected	Regional survey	(Tsrer et al., 1999a; Tsrer and Peretz-Alon, 2004)
France	<i>C. coccodes</i>	Presence reported	Field survey	(Andrison et al., 1997)
Germany	<i>C. coccodes</i>	Presence reported	First report	(Hars, 1871)
Germany	<i>H. solani</i>	Presence reported	Field survey	(Kutuzova et al., 2017)
Denmark	<i>C. coccodes</i>	Presence reported	Field experiment	(Pedersen et al., 2025)
India	<i>H. solani</i>	Presence reported	Field survey	(Tiwari et al., 2021)
Czech Republic	<i>H. solani</i>	40–80 % disease incidence	Field survey	(Sedláková et al., 2013)
Israel	<i>C. coccodes</i>	34 % seed-tuber lots affected; 22–30 % reduction in tuber yield	Seed-tuber survey; field trials	(Tsrer et al., 1999b)
Israel	<i>H. solani</i>	66 % moderately affected tubers and 33 % affected severely	Field survey	(Zimmerman-Gries and Blodgett, 1974)
Mauritius	<i>C. coccodes</i>	22 % of tuber surface area colonized	Field survey	(Takoore et al., 2023)
Mexico	<i>C. coccodes</i>	Presence reported	Field survey	(Pérez-Mora et al., 2020)
Norway	<i>C. coccodes</i>	59 % seed-tuber lots infected	Seed-tuber survey	(Nærstad et al., 2012)
Norway	<i>H. solani</i>	100 % of lots	Field survey	(Nærstad et al., 2012)
Poland	<i>H. solani</i>	Presence reported	Field survey	(Osowski, 2005)
Russia	<i>C. coccodes</i>	Presence reported	Field survey	(Yarmeeva et al., 2023)
Russia	<i>H. solani</i>	Presence reported	Field survey	(Chudinova et al., 2020)
Russia (Moscow)	<i>H. solani</i>	Presence reported	First report	(Wallroth, 1833)
South Africa	<i>C. coccodes</i>	Disease incidence of 41 %	Field experiment	(Denner et al., 1998)
South Africa	<i>C. coccodes</i>	30 % growers' fields affected; > 25 % yield loss	Field survey	(Van-der-Waals et al., 2016)
South Africa	<i>H. solani</i>	30 % of growers fields infected	Field survey	(Van-der-Waals et al., 2016)
Switzerland	<i>C. coccodes</i>	40 % of the tubers infected, colonization on 75 % of tubers	Field survey	(Massana-Codina et al., 2020)
Switzerland	<i>H. solani</i>	71 % of tubers infected	Field survey	(Massana-Codina et al., 2021)
Taiwan	<i>C. coccodes</i>	72 % tubers infected	Field survey	(Sheu et al., 2020)
Tunisia	<i>C. coccodes</i>	76–100 % tissue colonization by aggressive isolates	Greenhouse colonization trial	(Daami-Remadi et al., 2010)
United Kingdom	<i>C. coccodes</i>	Presence reported	Field survey	(Percival et al., 1999)
United Kingdom	<i>C. coccodes</i>	59 % tubers infected	Field survey	(Bradshaw, 2002)
United Kingdom	<i>C. coccodes</i>	75 % tubers infected	Field survey	(Read et al., 1995)
United Kingdom	<i>H. solani</i>	Presence reported	Field survey	(Jellis and Taylor, 1977)
United Kingdom	<i>H. solani</i>	61–98 % tubers infected	Field survey	(Read, 1991)
United Kingdom	<i>H. solani</i>	96 % tubers infected	Field survey	(Read et al., 1995)
U.S. (Idaho)	<i>C. coccodes</i>	Presence reported	Field survey	(Barkdoll, 1992)
U.S. (Idaho and Washington)	<i>C. coccodes</i>	Foliar inoculation caused premature vine death. Up to 30 % yield loss	Foliar inoculation trial	(Barkdoll, 1992; Eberlein et al., 1991)
U.S. (Indiana)	<i>C. coccodes</i>	Microclerotia in soil caused root/stolon damage. Up to 30 % premature vine death and yield loss	Soil-infestation trial	(Stevenson, 1976)
U.S. (North America)	<i>C. coccodes</i>	Presence reported	Regional survey	(Griffiths et al., 2010)
U.S. (North Dakota)	<i>C. coccodes</i>	80 % tubers infected	Field survey	(Aqeel et al., 2008; Pasche et al., 2010)
U.S. (Ohio)	<i>C. coccodes</i>	90 % tubers infected	Field survey	(Vrisman et al., 2017)
U.S. (Pacific Northwest)	<i>C. coccodes</i>	Visible foliar lesions and 43 % stem lesions	Field and glass-house inoculation trials	(Johnson, 1994)
U.S. (Washington)	<i>C. coccodes</i>	53–90 % tubers infected	Field survey	(Dung et al., 2012; Gundersen et al., 2025; Johnson et al., 2007; Nitzan et al., 2008)
USA (California)	<i>H. solani</i>	80 % tubers infected	Field survey	(Cunha and Rizzo, 2007)
USA (Colorado)	<i>H. solani</i>	50 % tubers infected	Field survey	(Hunger and McIntyre, 1979)
USA (New York)	<i>H. solani</i>	Up to 50 % tubers infected	Field survey	(Hunger and McIntyre, 1979; Jellis and Taylor, 1977)
USA (Wisconsin)	<i>C. coccodes</i>	94 % tubers infected	Field survey	(Mattupalli et al., 2013)
USA (Wisconsin)	<i>H. solani</i>	75 % tubers infected	Field survey	(Mattupalli et al., 2013)
Canada (Alberta)		Fungicide resistant isolates discovered from 15 of 32 farms surveyed (47 % overall; 76 % of southern farms; 21 % of northern farms infected)	Storage-facility survey	(Holley et al., 1996)

with *Pseudomonas putida* PM1 showing highest inhibition of 80 % followed by *Kocuria rosea* with an inhibition of 76 % (Elson et al., 2007; Lysøe et al., 2017; Martinez et al., 2002; Michaud et al., 2007). Moreover, isolation of bacterial isolates from disease suppressive soil from Mexico has yielded different strains of *Streptomyces* sp. showing antagonism of 60–70 % against *H. solani* under *in vitro* conditions

(Evangelista-Martínez, 2014). This indicates an important role of rhizospheric and soil microbes in establishing natural defense against pathogens, likely through mechanisms involving root exudate-mediated enrichment of beneficial microbes that antagonize pathogens or by boosting plant immunity (Du et al., 2024). The efficacy of biocontrol activity of these living microbes depends on varied factors such as doses,

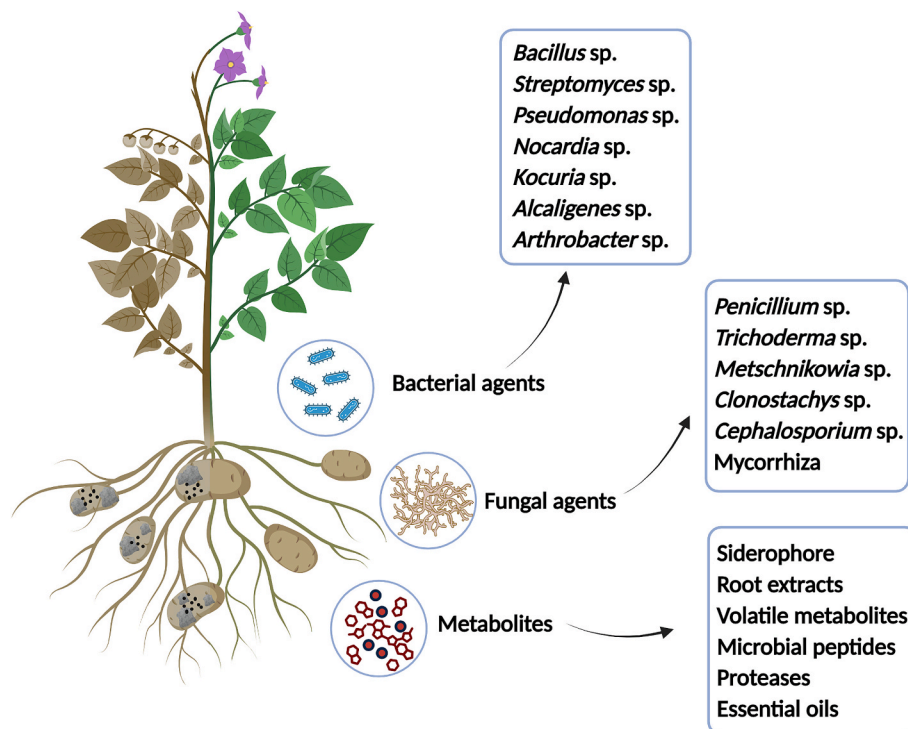


Fig. 4. Biological management of silver scurf and black dot in potato using biocontrol agents and bioprotectants. This figure was created with BioRender (<https://BioRender.com/vpnr3v0>).

temperature, application timing etc. with optimal results observed at different specific conditions (Martinez et al., 2002; Michaud et al., 2007). Species such as *Arcanobacterium haemolyticum*, *Herbapirillum autotrophicum*, *Bacillus mycoides*, *Kocuria rosea*, *Rhodococcus erythropolis*, *Streptomyces griseus*, *Bacillus cereus*, and *Pseudomonas putida* were most effective at 10 to 15 °C under *in vitro* conditions in tuber inoculation assay, making them suitable for post-harvest storage applications. In contrast, *Rhodococcus globerulus*, *Kocuria varians*, and *Alcaligenes piechaidii* showed peak efficacy at 24 °C, indicating its potential as seed tuber treatments for reducing disease during planting and growing seasons. Notably, *Arthrobacter oxydans* demonstrated consistent disease suppression of approximately 70 % at both 10 °C and 24 °C, highlighting its versatility across using it in different phases of potato production (Martinez et al., 2002; Michaud et al., 2007). Further studies examining the role of antibiosis in antagonistic bacteria suppression of *H. solani* under dual culture assay and antagonist derived exudates on *in vitro* conidial germination identified *Alcaligenes piechaidii*, *Aquaspirillum autotrophicum*, *Cellulomonas fimi*, *Pseudomonas chlororaphis*, *Pseudomonas fluorescence*, *Kocuria varians*, *Pseudomonas putida* (strains 94–19 and E-30) and *Streptomyces griseus* as effective direct antagonists showing a fungistatic and fungitoxic effect ranging from 5–100 % with highest fungistatic effect shown by *Pseudomonas fluorescence* (73.3 %) and fungitoxic effect shown by *Kocuria varians* (45.1 %) compared to uninoculated control (Martinez et al., 2006). Assessing simultaneous seed dressing and soil application of biocontrol products as a preventive strategy prior to planting of potatoes in the field against *H. solani* showed that among the treatments, Serenade ASO (biological product derived from *Bacillus amyloliquefaciens* QST 713) showed highest protective efficacy (45.2 % to 56.6 %) in reducing silver scurf severity followed by Biogen rewital (biological product derived from microbial consortia of cellulolytic, nitrifying, sanitary, lipolytic bacteria) showing a moderate level protection of 25.2–27.7 % and UGMax soil conditioner (biological product derived from microbial consortia of acid bacteria, photosynthetic bacteria, *Azotobacter*, *Pseudomonas*, actinomycetes, and yeasts) with slightly lower efficiency of 16–22 % (Gleń-Karolczyk et al., 2022).

In the context of managing *C. coccodes*, recent studies have only

identified a few bacterial species with effective biocontrol capabilities against black dot. Notably, strains such as *Bacillus amyloliquefaciens* DA12, *Brevibacillus halotolerans* B-4359, *Lactiplantibacillus acidophilus* and *Streptomyces* strain PR22 have shown promising suppression rates of over 50 % against black dot under *in vitro* petri plate assays with *Lactiplantibacillus acidophilus* exhibiting a remarkable 90 % reduction in the growth of *C. coccodes* (Kim et al., 2023, 2021; Lee et al., 2017; Steglińska et al., 2022c; Yutthasin et al., 2015). Only few studies reported on the use of biocontrol products against *C. coccodes* except combined spray application of *Streptomyces* derived formulations like Mycostop (derived from *S. griseoviridis* K61) and Actinovate (derived from *S. lydicus* WYEC108) at the seeding stage simultaneous with pathogen inoculation in the greenhouse followed by field transplantation showed a significant reduction in the *C. coccodes* incidence on harvested fruit to 9 % compared to 36 % in the *C. coccodes* only inoculated tomato plants (Cuppels et al., 2013). Although the biocontrol potential of several bacterial strains like *Bacillus subtilis*, *Streptomyces* sp. etc. against silver scurf and black dot has been documented (Table 2), most investigations have not advanced beyond whole tuber assays, and the few extended trials have primarily focused on the plants other than the potato. This research gap calls for dedicated studies under field conditions to confirm efficacy of the biocontrol agents in potato crops. Future efforts should prioritize evaluating these strains and derived products during distinct production phases and developing optimized, practical application protocols for consistent field success.

5.1.2. Fungal biocontrol agents

Only a limited number of studies have explored the use of fungal biocontrol agents as living microbes against *H. solani* and *C. coccodes*. Research on different *Trichoderma* species, including *T. viride*, *T. koningi*, *T. polysporum*, *T. harzianum*, and *T. hamatum* isolated from the soil and rhizosphere of potato crop has been identified antagonistic to the growth of *H. solani* under *in vitro* condition with highest biotic effect shown by *Trichoderma viride* followed by *Trichoderma polysporum* (Kurzawińska, 2006). In addition, studies have revealed that the fungus *Acremonium strictum* from petri plates demonstrated antagonistic effects against

Table 2
Summary table showing different biocontrol and bioprotectants used against black dot and silver scurf.

Sl no	Category	Biocontrol agent	Inhibition (%)	Class	Pathogen	Reference
1	Live biocontrol agents	<i>Pseudomonas putida</i>	70.4	Bacteria	<i>H.solani</i>	(Elson et al., 2007)
2		<i>Xanthomonas campestris</i>	57	Bacteria	<i>H.solani</i>	(Elson et al., 2007)
3		<i>Nocardia globerula</i>	76	Bacteria	<i>H.solani</i>	(Elson et al., 2007)
4		<i>Alcaligenes piechaudii</i>	51,3	Bacteria	<i>H.solani</i>	(Michaud et al., 2007)
5		<i>Aquaspirillum autotrophicum</i>	73.3	Bacteria	<i>H.solani</i>	(Michaud et al., 2007)
6		<i>Arthrobacter oxydans</i>	66.7	Bacteria	<i>H.solani</i>	(Michaud et al., 2007)
7		<i>Arcanobacterium haemolyticum</i>	66.7	Bacteria	<i>H.solani</i>	(Michaud et al., 2007)
8		<i>Bacillus mycoides</i>	73.3	Bacteria	<i>H.solani</i>	(Michaud et al., 2007)
9		<i>Cellulomonas fimi</i>	48.1	Bacteria	<i>H.solani</i>	(Martinez et al., 2002)
10		<i>Kocuria rosea</i>	76.7	Bacteria	<i>H.solani</i>	(Michaud et al., 2007)
11		<i>Pseudomonas chlororapis</i>	Not mentioned	Bacteria	<i>H.solani</i>	(Martinez et al., 2006)
12		<i>Rhodococcus erythropolis</i>	51.9	Bacteria	<i>H.solani</i>	(Martinez et al., 2002)
13		<i>Kocuria varians</i>	70.4	Bacteria	<i>H.solani</i>	(Martinez et al., 2002)
14		<i>Pseudomonas fluorescens</i>	68	Bacteria	<i>H.solani</i>	(Martinez et al., 2002)
15		<i>Rhodococcus globerulus</i>	55.6	Bacteria	<i>H.solani</i>	(Martinez et al., 2002)
16		<i>Paenibacillus polymyxa</i> S-13	30	Bacteria	<i>H.solani</i>	(Gajda and Kurzawińska, 2004)
17		<i>Bacillus cereus</i>	63	Bacteria	<i>H.solani</i>	(Martinez et al., 2002)
18		<i>Streptomyces griseus</i>	52.5	Bacteria	<i>H.solani</i>	(Michaud et al., 2007)
19		<i>Streptomyces</i> sp. CACIS-2.17CA	71	Bacteria	<i>H.solani</i>	(Evangelista-Martinez, 2014)
20		<i>Bacillus amyloliquefaciens</i> DA12	57.9	Bacteria	<i>C. coccodes</i>	(Lee et al., 2017)
21		<i>Bacillus velezensis</i> HKB-1	70	Bacteria	<i>C. coccodes</i>	(Kim et al., 2021)
22		<i>Brevibacillus halotolerans</i> B-4359	51.7	Bacteria	<i>C. coccodes</i>	(Kim et al., 2023)
23		<i>Lactiplantibacillus plantarum</i> KB2	75	Bacteria	<i>C. coccodes</i>	(Steglińska et al., 2022)
24	<i>Bacillus</i> sp. SW29-2	28.5	Bacteria	<i>C. coccodes</i>	(Han, 2017)	
25	<i>Streptomyces</i> -PR22	88	Bacteria	<i>C. coccodes</i>	(Yutthasin et al., 2015)	
26	<i>S. lydicus</i> WYEC108 + <i>P. fluorescens</i> A506	74	Bacterial consortia	<i>C. coccodes</i>	(Cuppels et al., 2013)	
27	<i>Acremonium strictum</i>	40	Fungus	<i>H.solani</i>	(Rivera-Varas et al., 2007)	
28	<i>Trichoderma</i> sp.	41.5	Fungus	<i>H.solani</i>	(Kurzawińska, 2006)	
29	<i>Clonostachys rosea</i>	95	Fungus	<i>H.solani</i>	(Lysoe et al., 2017)	
30	<i>Metschnikowia pulcherrima</i>	100	Fungus	<i>C. coccodes</i>	(Steglińska et al., 2022)	
31	<i>Penicillium raperi</i>	Not mentioned	Fungus	<i>C. coccodes</i>	(Lichtner et al., 2022)	
32	<i>R. irregularis</i> + <i>P. brassicacearum</i>	21	Bacteria + Fungus	<i>C. coccodes</i> , <i>H. solani</i>	(Darbon et al., 2024)	
33	<i>Bacillus subtilis</i> GB03 + <i>R. solani</i> AG-3(Bs69 and Rhs1A1)	24	Bacteria + Fungus consortia	<i>H.solani</i>	(Larkin, 2020)	
34	Biocontrol products	Serenade ASO	40.2	<i>Bacillus subtilis</i>	<i>H.solani</i>	(Gleń-Karolczyk et al., 2022)
35	Bio-Save 10LP		68	<i>Pseudomonas syringae</i>	<i>H.solani</i>	(Al-Mughrabi et al., 2013)
36	Biogen Rewital		26.2	Microbial consortia of (cellulolytic, nitrifying, sanitary, lipolytic) bacteria	<i>H.solani</i>	(Gleń-Karolczyk et al., 2022)
37	Em Farma™ Probiotics		20.9	Microbial consortia	<i>H.solani</i>	(Gleń-Karolczyk et al., 2022)
38	UG Max soil conditioner		23.1	Microbial consortia of acid bacteria, photosynthetic bacteria, <i>Azotobacter</i> , <i>Pseudomonas</i> , <i>actinomycetes</i> , and yeasts	<i>H.solani</i>	(Gleń-Karolczyk et al., 2022)
39	MycZoom		Not mentioned	Mycorrhiza	<i>H.solani</i>	(Loit et al. 2023)
40	Polyversum WP		36.3	<i>Pythium oligandrum</i>	<i>H.solani</i>	(Gleń-Karolczyk et al., 2022)

(continued on next page)

Table 2 (continued)

Sl no	Category	Biocontrol agent	Inhibition (%)	Class	Pathogen	Reference
41		Mycostop	40	<i>Streptomyces griseoviridis</i> K61	<i>C.coccodes</i>	(Cuppels et al., 2013)
42		Actinovate	40	<i>S. lydicus</i> WYEC108	<i>C.coccodes</i>	(Cuppels et al., 2013)
43	Bioprotectants	2E-hexenal	100	Plant VOC	<i>C. coccodes</i> , <i>H. solani</i>	(Wood et al., 2013)
44		Thymol 80 ppm	99.82	Essential Oils	<i>H.solani</i>	(Kmoche et al., 2023)
45		Carvacrol 100 ppm	40.80	Essential Oils	<i>H.solani</i>	(Kmoche et al., 2023)
46		Cinnamaldehyde 120 ppm	93.56	Essential Oils	<i>H.solani</i>	(Kmoche et al., 2023)
47		Compost water extracts	65	Crude metabolites	<i>C.coccodes</i>	(Sang and Kim, 2011)
48		Curcuminoids (bisdemethoxycurcumin, curcumin)	87–100	<i>Curcuma longa</i> metabolite	<i>C.coccodes</i>	(Almada-Ruiz et al., 2003)
49		Guava Wood Vinegar 3 %	100	<i>Psidium guajava</i> Wood extract	<i>C. coccodes</i>	(El-Fawy et al., 2023)
50		Curcumin	47	<i>Curcuma longa</i> rhizome extract	<i>C. coccodes</i>	(Massana- Codina, 2020)
51		Anthraquinones and phenylpropanoid derivatives	35	<i>Rheum palmatum</i> roots extract	<i>C. coccodes</i>	(Massana- Codina, 2020)
52		Frangulin B	45	<i>Frangula alnus</i> bark extract	<i>C. coccodes</i>	(Massana- Codina, 2020)
53		5-Hydroxymethylfurfural	100	Garlic water	<i>C. coccodes</i>	(Massana- Codina, et al., 2022)
54		Culture Filtrate	59.7	<i>Bacillus cereus</i>	<i>H.solani</i>	(Martinez et al., 2006)
55		Isobutyric acid	100	VOC from <i>Muscodor albus</i>	<i>H.solani</i>	(Corcuff et al., 2011)
56		Culture Filtrate	24.8	<i>Kocuria rosea</i>	<i>H.solani</i>	(Martinez et al., 2006)
57		Culture Filtrate	73.3	<i>Pseudomonas fluorescens</i>	<i>H.solani</i>	(Martinez et al., 2006)
58		Vitavax 2000 FS (0.1 %)	99.7	Chitosan	<i>H.solani</i>	(Kurzawińska and Mazur, 2020)
59		Biochikol 020 PC (2.0 %)	74	Chitosan	<i>H.solani</i>	(Kurzawińska and Mazur, 2020)
60		ExPro138	50	Extracellular proteases from <i>Streptomyces phaeopurpureus</i>	<i>C.coccodes</i>	(Palaniyandi et al., 2013)
61		Antifungal Peptide 50 μM	100	<i>Saccharomyces cerevisiae</i>	<i>C.coccodes</i>	(Jones and Prusky, 2007)
62		2-ethyl-1-hexanol	100	VOC from <i>Bacillus mojavensis</i> ZA1	<i>C. coccodes</i>	(Wei et al., 2023)
63		Crinipellin A	65	Culture filtrate from <i>Crinipellis</i> sp.	<i>C. coccodes</i>	(Han et al., 2018)
64		Siderophore	41.7	Metabolite from <i>Nocardia mangyaensis</i>	<i>C. coccodes</i>	(Khilyas et al., 2024)
65		Cell free extract	44	<i>Penicillium</i> sp.	<i>C. coccodes</i>	(Hassine et al., 2022)
66		Cell free extract	58	<i>Gliocladium catenulatum</i>	<i>C. coccodes</i>	(Hassine et al., 2022)
67		Cell free extract	84	<i>Gliocladium virens</i>	<i>C. coccodes</i>	(Hassine et al., 2022)

H. solani, reducing sporulation from 65 % to 35 %, spore germination from 53 % to 43 %, and mycelial growth from 40 % to 32 % compared to pure *H. solani* cultures across different temperature and humidity conditions with highest reduction in the germination of spores observed under 5 °C and 95 % RH indicating the application of *Acremonium strictum* in the post-harvest management of silver scurf as a protective agent in healthy tubers. Furthermore, *A. strictum* decreased *H. solani* conidia production on mini tubers, thereby lowering the pathogen inoculum load and potential for infection, though it showed no curative effect on infected tubers. These findings indicate that *A. strictum* functions as a mycoparasite and could potentially be a biocontrol candidate for preventing silver scurf disease as a seed dressing candidate prior to planting of the tubers (Rivera-Varas et al., 2007). Kurzawińska and Mazur (2006) demonstrated the effectiveness of chitosan formulation Biochikol 020 PC and Polyversum (*Pythium oligandrum*) in managing *H. solani* infestation. Under *in-vitro* conditions, Biochikol 020 PC (2.0 %) exhibited the highest inhibition of mycelium linear growth, with suppression rates of approximately 74 % (Kurzawińska, 2006). In field trials, the most effective protection was observed when a combination of Polyversum and Biochikol 020 PC were used for tuber dressing and supplemented with four foliar sprays during the growing season

(Kurzawińska, 2006). Recent study has also showed the efficiency of a seed coating of arbuscular mycorrhizal (*Rhizophagus* spp) product Mycozoom to defend against silver scurf (Loit et al., 2023).

Even though studies on fungal biocontrol agents against *C. coccodes* seems to be sparse, recent findings have highlighted the potential of the yeast *Metschnikowia pulcherrima*, which achieved complete inhibition of *C. coccodes* infestation on potato tubers when applied simultaneously with the pathogen (Steglińska et al., 2022b). Analysis of the metabolite profile of *M. pulcherrima* further revealed that compounds such as pulcherrimin, organic acids, ethanol, glycerol, leucine arylamidase, valine arylamidase, α - and β -glucosidase, and esterases are likely contributors to its strong antagonistic effects (Steglińska et al., 2022b). Despite promising *in vitro* results, the application of fungal biocontrol agents (Table 2) such as *Trichoderma* spp., *Acremonium strictum*, and *Metschnikowia pulcherrima* remains largely underexplored in field conditions, particularly with respect to their integration at specific stages of the potato production cycle such as seed treatment before planting or post-harvest tuber protection.

5.1.3. Microbial consortia used for biocontrol of tuber blemish diseases

Considering the individual inhibitory effects exhibited by various

fungus and bacterial species, recent efforts have explored the use of microbial consortia utilizing combinations of multiple fungal and bacterial species or strains for biocontrol applications (Nunes et al., 2024). Such consortia could offer advantages over single species applications by overcoming some biological limitations such as narrow host specificity, inconsistent field performance or limited survival in the rhizosphere associated with individual microbes (Nunes et al., 2024). In addition, combining different species increases stability across diverse ecological and environmental conditions and allows for multiple biocontrol mechanisms to target pathogens simultaneously (Trivedi et al., 2021). Interest has also grown in combining microbial species that do not naturally occupy the same ecological niche (Arif et al., 2020). Bacteria isolated from potato tubers on defense against black dot have identified that synergistic combination of *Pantoea agglomerans* (epiphytic, tuber surface) and *Bacillus subtilis* (endophytic, internal tissues) in a 4:6 ratio, applied preventively to potato tuber slices, inhibited *C. coccodes* by 68 % and enhanced defense responses via increased peroxidase and superoxide activity (Zhang et al., 2025). In contrast, attempts to control *H. solani* and *C. coccodes* using other combinations, such as *Rhizophagus irregularis* with *Pseudomonas brassicacearum*, and *Bacillus subtilis* GB03 with hypovirulent strains of *Rhizoctonia solani* AG-3 (Bs69 and Rhs1A1) showed lower efficacy, with inhibition rates of only 20–25 % (Darbon et al., 2024; Larkin, 2020). This reduced effectiveness may stem from microbial incompatibility or competition with native organisms, and difficulties in adapting to specific environmental conditions (Arif et al., 2020). Prioritising and optimizing microbial consortia by identifying compatible microbial combinations that enhance biocontrol efficacy might overcome these limitations in future. Advances in metagenomics, transcriptomics, and metabolomics could potentially also aid in elucidating the mechanisms underlying successful biocontrol interactions, guiding the selection of optimal microbial combinations.

However, apart from its various benefits, practical challenges could impede their implementation. The validation and optimization of consortia designed *in silico* and *in vitro* across various laboratory conditions could not substantiate the results until it is experimented in reproducible field trials (Ayaz et al., 2023). Moreover, establishing mass production, downstream processing, and storage protocols for each microbe in a consortium would demand considerably more resources and investments compared to producing single strain microbial biocontrol agents in a commercial setting (Nunes et al., 2024). Registering assembled consortia as plant protection products will also add further legal complexities in its introduction to the market (Abbas et al., 2022). For example, in the European Union, regulations require a comprehensive risk assessment of each active ingredient before a product can be registered (Robin and Marchand, 2019). In this context, strategies to shape the indigenous microbiota or enhancing the efficiency of already approved commercial biocontrol may offer advantages over the introduction of new consortia. On the other hand, an adapted legislative framework that is tailored to accommodate novel disease control systems in permitted settings would benefit both society and the environment as a whole (Köhl et al., 2019).

5.2. Microbial and plants derived metabolites as bioprotectants

Biological control emphasizes the use of living organisms to manage pathogens, so metabolites derived from microbes or plants do not fall under this definition, because they are non-living chemical products (Collinge et al., 2022). These substances, although capable of suppressing pathogens, cannot reproduce or persist in the environment (Collinge et al., 2022). Unlike living microbes, which can colonize and adapt to the plant rhizosphere, metabolites typically degrade and lose activity over time, requiring repeated applications during the crop production cycle unless they are capable of triggering a systemic and sustained plant defense response (Köhl et al., 2019). Secondary metabolites produced by plants and microbes include a wide array of bioactive compounds with

diverse chemical structures and functions, playing a crucial role in plant defense and microbial antagonism (Bano et al., 2023). In plants, these metabolites are often synthesized as part of complex defense pathways activated in response to biotic stressors, such as pathogen effectors (Bano et al., 2023). Key groups of plant secondary metabolites with antimicrobial properties include alkaloids, terpenoids, phenolics, flavonoids, and saponins (Al-Khayri et al., 2023). Each class has distinct biochemical activities, some disrupt pathogen cell membranes, others interfere with metabolic processes, and some inhibit spore germination or fungal hyphal growth (Al-Khayri et al., 2023).

Microbes, including bacteria and fungi produce secondary metabolites that serve as potent antimicrobial agents against plant pathogens. For instance, microbes produce lipopeptides, phenazines, and siderophores that inhibit pathogens directly or stimulate plant immune responses (Ayaz et al., 2023). Extraction and formulation of these natural compounds can lead to effective plant disease management solutions by inducing systemic resistance in plants, providing prolonged protection against multiple pathogens and are typically less harmful to non-target organisms and degrade more readily in the environment (de Cenobio-Galindo, 2024). Advances in biotechnology and chemical ecology are making it increasingly feasible to isolate, characterize, and produce these bioactive metabolites on a larger scale to open the way for commercial applications in sustainable agriculture.

5.2.1. Plant metabolites

Plant extracts rich in antimicrobial secondary metabolites may present an approach for controlling plant diseases. These compounds are naturally abundant, biodegradable, and environmentally safe (Bano et al., 2023). Numerous plant extracts have been tested and explored for their potential against *C. coccodes* and *H. solani*. Among them, plant volatile organic compound 2E-hexenal (metabolite from bananas, tomatoes, and other fruits as an aroma volatile associated with a green or grassy smell) was the most effective at a dose of 5 ppm providing complete inhibition of both the pathogens on dual confrontation assays. Studies have showed that a concentration of 2.5 ppm of 2E-hexenal could completely inhibit the germination of *H. solani* conidia under *in vitro* condition indicating its efficiency to manage these diseases in post-harvest conditions (Wood et al., 2013). In an attempt to evaluate the antifungal efficiency of essential oils derived from various common plant species including *Cinnamomum*, *Origanum* sp., *Thymus* sp., *Coriandrum sativum*, and *Mentha piperita*, a range of key oil components such as pinene, carvacrol, cinnamaldehyde, D-carvone, eucalyptol, L-linalool, L-menthol, L-menthone, (R)- (+)-limonene, and thymol have showed that tuber dressing with a 2 % essential oil solution for 2 s, and fumigation using 4.2 g of essential oil per 100 ml/m³ for 60 days at 10–15 °C and 99 % relative humidity were effective in reducing the sporulation intensity of *H. solani* on tuber surface with thymol, carvacrol, and cinnamaldehyde as the major compounds reducing the sporulation intensity with dressing (97.44–100 %) compared to fumigation (86.69–97.73 %) (Kmoche et al., 2023). On the other hand, the spray application of curcuminoids from *Curcuma longa* in a range 0.4–100 µg/ml effectively inhibited the mycelial growth and spore germination of *C. coccodes*, of which 20 µg/ml bisdemethoxycurcumin showed 100 % inhibitory activity under *in vitro* assay. Under greenhouse conditions, only spray application of 500 and 1,000 µg/ml demethoxycurcumin exhibited 92–95 % suppression of *C. coccodes* in red pepper (Cho et al., 2006). Moreover the non-phytotoxic effects of these compounds even at higher concentrations of 2000 µg/mL, highlights their potential as effective bioprotectants for post-harvest storage of potatoes against black dot (Cho et al., 2006). Post harvest curative application of 10 g/L of plant extracts like *Curcuma longa* and *Frangula alnus* extracts have also manifested a 43 % and 31 % reduction in silver scurf symptoms comparable to that in chemical fungicide treatment, while only *C. longa* extract showed significant control efficiency (47 %) in controlling black dot on potato tubers (Massana-Codina, 2020). These findings are particularly important, as majority of harvested tubers are

asymptomatic, and curative treatments could effectively reduce the risk of secondary infections during potato storage.

Recent strategies on using wood vinegar, a byproduct of charcoal production of guava trees revealed that foliar spray at the concentration of 2 % and 3 % significantly decreased the disease severity index (DSI) of black dot in all disease parameters, including stem colonization (22–23 %), root covering with sclerotia (18–22 %), and wilt percentage (27–33 %) in potato plants under greenhouse conditions (Elfawy et al., 2023). Furthermore, screening of 22 plant water extracts, 22 water-glycol extracts, and 3 subcritical carbon dioxide extracts against *C. coccodes* identified garlic water extract as the most potent inhibitor (100 % efficacy), both *in vitro* and *in situ* assay on potato tuber slices, with minimum inhibitory concentration of 12.5 mg/mL. Metabolite analysis revealed that 5-hydroxymethylfurfural (33.24 %) was the major bioactive compound responsible for its inhibitory effect (Steglińska et al., 2022a). Even though plant derived metabolites represent a promising source of antifungal compounds for the management of black dot and silver scurf (Table 2), their potential non-target effects must be carefully evaluated when potatoes are used for human consumption. Secondary metabolites such as alkaloids, phenolics, and furan derivatives can persist on or within tuber tissues, raising questions about dietary exposure and toxicological safety. For example, 5-hydroxymethylfurfural identified as a major inhibitory compound in garlic extract, occurs naturally in heat-processed foods but has been linked to cytotoxic and genotoxic effects at high concentrations (Abraham et al., 2011).

5.2.2. Microbial metabolites

Numerous bioactive compounds produced by microbes, including Actinobacteria and fungi, hold significant potential for protecting plants against phytopathogens (de Cenobio-Galindo, 2024). There are only a few studies on exploitation of microbial metabolites used as antagonist against *H. solani* and *C. coccodes*.

5.2.2.1. Volatile metabolites. Volatile organic compounds (VOCs) from microbial sources can exert strong fungistatic or fungicidal effects. Analysis of volatile compounds such as 2-Ethyl-1-hexanol, 2-methyl-1-butanol, 4,4- (1-methylethylidene) bisphenol and 2,3-butanediol derived from *Bacillus mojavensis* ZA1 showed 52 – 100 % efficiency in controlling the growth and conidial germination of *C. coccodes* with complete suppression showed by 2-Ethyl-1-hexanol and 2-methyl-1-butanol under *in vitro* conditions (Wei et al., 2023).

5.2.2.2. Solvent-extracted metabolites. Ethyl acetate (5 %) and chloroform (5 %) extracts of *Penicillium* and *Gliocladium* species have been reported to reduce anthracnose decay by 11–85 %, with the ethyl acetate extract from *Penicillium* sp. CH6 showing the highest reduction (85 %), suggesting that such extracts may also have comparable potential against black dot on potato tubers (Hassine et al., 2022). Moreover methanolic culture filtrates of bacterial exudates from *B.cereus*, *Kocuria rosea* and *Pseudomonas fluorescens* have inhibited conidial germination with inhibition rates of 59.7 %, 24.8 %, and 73.3 % against *H. solani* under *in vitro* conditions indicating their relevance as candidates for pre- or post-harvest treatments (Martinez et al., 2006).

5.2.2.3. Extracellular enzymes and cell-free extracts. Cell-free extracts (20 %) from *Penicillium* spp. (MC1, CH6), *Gliocladium virens* and *G. catenulatum* (Gc1) reduced black dot severity on tomato fruits by 20–25 % with highest reduction in severity of 25 % showed by cell-free filtrates from *Penicillium* sp. (MC1, CH6) and *G. catenulatum* (Gc1) cultures when applied preventively (Hassine et al., 2022). Although modest, these reductions reflect the potential of enzymatic or metabolite-rich extracts to interfere with early infection development.

A well-characterized example is the extracellular protease from *Streptomyces phaeoauripureus* ExPro138, which inhibited *C. coccodes* spore germination completely at 100 µg/mL, reduced adhesion to

polystyrene surfaces by 50–60 %, and suppressed appressorium formation. When applied to tomato fruits, the protease reduced anthracnose incidence by 50 % (Palaniyandi et al., 2013), demonstrating that enzymatic disruption of infection structures can be a powerful disease control mechanism.

These findings (Table 2) underline the potential of microbial metabolites in preventive treatments and targeted inhibition of fungal infection mechanisms prior to the planting or post-harvest management of black dot and silver scurf. However, most studies have been limited to *in vitro* conditions with little focus on field level efficacy and formulation stability under variable environmental conditions. Furthermore, the mode of action of many microbial metabolites is not fully understood, particularly their interactions with plant defence pathways and their long-term persistence in the soil. The combined use of microbial metabolites, either together or with biocompatible carriers, remains underexplored.

6. Other non-chemical management strategies

Since disease symptoms typically appear during the later stages of storage, visual-based methods are inadequate, as the pathogens may have already spread by the time symptoms become visible. To tackle these obstacles, researchers have been investigating on alternative nucleic acid based and advanced imaging technology to diagnose these diseases providing benefits such as increased sensitivity, precision, and specificity compared to methods relying on traditional approaches utilizing visual scoring of symptoms to exclude the infected tubers from carrying to the storage and screening of seed tubers before planting (Wang et al., 2023). Advanced diagnostic tools like electronic nose (e-nose) sensors integrated with PCR, CRISPR based assays, and imaging techniques using CNN and FT-IR have shown strong potential for early pathogen detection in tubers (Khlaif et al., 2024; Khmeleva et al., 2024; Lin et al., 2024; Oppenheim et al., 2019). For example, e-nose systems have successfully identified *Pectobacterium* through volatile profiling and *Colletotrichum coccodes* in tomatoes, CRISPR-based diagnostics have enabled sensitive detection of *Clavibacter sepedonicus*, the causal agent of ring rot in potatoes, convolutional neural networks (CNN) and Fourier transform infrared (FT-IR) has also produced results on rapid, inexpensive, and reliable monitoring system to detect occurrence of blemish diseases with a classification accuracy ranging from 83 % to 96 % (Khlaif et al., 2024; Khmeleva et al., 2024; Lin et al., 2024; Oppenheim et al., 2019). These successes highlight the potential of adapting such technologies for early detection of black dot and silver scurf, thereby reducing the risk of secondary infections during storage and ensuring the exclusion of infected tubers from planting material. However, the most critical potato storage management is maintaining the optimal lower temperature (3–4 °C) and humidity (80–90 %RH) without allowing excess moisture, as moisture can increase the disease development even at lower temperatures (Frazier et al., 1914; Rodriguez et al., 1996).

Another approach could be breeding the resistance cultivars. A recent greenhouse based resistance screening of five potato cultivars (Cheyenne, Ditta, Erika, Gwenne, and Lady Felicia) revealed that Erika and Gwenne were the least susceptible to black dot, and both showed silver scurf severity below 5 % (Massana-Codina, 2020). In contrast, Lady Felicia exhibited the highest susceptibility to black dot with 45 % disease severity, while Lady Christl was the most affected by silver scurf, showing 28 % disease severity (Massana-Codina, 2020). Further investigation is required to understand the resistance of different cultivars specific to black dot and silver scurf. However, breeding could remain an ongoing effort due to the rapid evolution of pathogens, which can overcome resistance, rendering plants susceptible (Khan et al., 2008). For instance, the incorporation of these resistance genes could be a possible mechanism to investigate its broad effectiveness against black dot and silver scurf. Tomato plants modified with pepper 9-Lipoxygenase (9-LOX) gene, pectin lyase and p35 gene exhibited immunity to

AAL-toxin conferring protection against *C. coccodes* (Ben-Daniel et al., 2010; Hwang and Hwang, 2010). Targeting alterations in the specific reported genes in potatoes can have a greater impact in improving resistance of the crop against black dot and silver scurf, while off-target mutations and fitness costs due to their linkage with other desirable genes of plant growth and development should also be considered while adopting this strategy (Ahmad et al., 2020). Although gene editing is a powerful technology, reluctance in its acceptance by consumers and ecologists also poses a serious concern and needs to be taken into consideration while adopting this technology (Hahn and Nekrasov, 2019).

7. Proposed integrated non-chemical management strategies for black dot and silver scurf in potato

An effective, eco-friendly non-chemical management strategy for black dot (*C. coccodes*) and silver scurf (*H. solani*) in potatoes should continue from planting to marketing by selecting certified, disease-free resistant seed tubers and choosing a field following a minimum three to four year rotation with non-compatible hosts for the pathogens like winter oilseed rape or high GSL mustard could reduce the initial inoculum levels in soil (Johnson and Cummings, 2015; Massana-Codina et al., 2021). In addition, incorporation of PCR pre-planting screenings to confirm the absence of pathogen in seed tubers and planting soil along with the incorporation of organic amendments such as well-composted manures, suppressive soils or green manures rich in antagonistic microorganisms enhance microbial competition and suppresses pathogen survival (Cullen et al., 2002; Khmeleva et al., 2024; Martinez et al., 2002).

Pre-planting activities like reduced tillage, proper soil drainage and avoiding excessively cool, wet soils reduce pathogen spore germination and colonization in the emerging roots, and the use of biocontrol agents such as *Trichoderma sp.* or *Bacillus sp.* formulations coated onto seed tubers can further inhibit subsequent tuber infection (Napolitano et al., 2024; Zhang et al., 2023). During the growing season, maintaining balanced nutrition, especially with calcium and silicon fortifies tuber skin integrity and impairs pathogen penetration, while careful irrigation management (e.g., drip rather than overhead systems) minimizes water splashing and reduces spore dispersal (Wadas and Kondraciuk, 2023). At harvest, gentle handling of tubers using padded harvesters to avoid tuber skin abrasions, prompt removal of soil residues, and field sanitation collecting and destroying haulm piles limit the spread of inoculum into the subsequent seasons (Massana-Codina, 2020). Moreover early detection of these pathogens in the asymptomatic tubers could be utilized using sensitive molecular techniques to keep infected lots out of storage, thereby minimizing secondary infections (Cullen et al., 2002; Khmeleva et al., 2024).

In the storage phase, curing at moderate temperatures (12–15 °C) and high relative humidity (90–95 %) encourages suberization of skins, creating a stronger barrier to pathogen colonization (Frazier et al., 1998). Moreover, storing of tubers under cool (3–4 °C), intermittent or reduced-speed ventilation, and moderately dry conditions (85–90 % RH) in pathogen resistant plywood boxes could suppresses pathogen growth without inducing excessive tuber dehydration. Routine monitoring of storage conditions and regular inspection of tubers for early lesions allows quick removal of any affected tubers, preventing pathogen buildup (Frazier et al., 1998). Finally, in the post-storage period, treatment of seed lots with biocontrol dips could prevent subsequent infection, while on-farm sanitation of storage and handling equipment between seasons interrupts the disease cycle entirely (Elson et al., 2007; Wei et al., 2023). For table potatoes to the market, modifications to the existing sorting system such as incorporating optical sorting along with machine learning like CNN to detect the blemish disease, replacing the potato washing water frequently in washing tanks, and thorough drying of tubers before packing can effectively reduce pathogen proliferation (Sanzo-Miró et al., 2023).

Thus, a holistic approach combining cultural practices, biological control agents, and physical measures at various phases of potato production (Fig. 5) could sustainably suppress both black dot and silver scurf effectively.

8. Conclusion and future prospects

Black dot and silver scurf are two blemish diseases of global concern that significantly reduce the market value and quality of potato tubers. The growing demand for chemical free food production, coupled with emergence of resistant strains to synthetic fungicides, underscores the urgency for sustainable and effective chemical free disease management strategies. Primarily it lies in the careful selection of disease free seed tubers, resistant cultivars and planting tubers in pathogen free soil complemented by early pathogen detection through advanced molecular methods. This could be further strengthened by incorporating biological control agents alongside other strategies, either before planting or during the post-harvest stage. The effectiveness of biocontrol agents is influenced by various factors, including environmental conditions, application timing, and formulation stability. Several bacterial and fungal strains have demonstrated significant inhibition of black dot and silver scurf *in vitro* and under controlled environments. However, many of these promising candidates require further validation in field conditions specific to different production stages.

Similarly, the use of plant and microbe derived metabolites and essential oils may be a management tool, though their large-scale implementation should consider issues like volatility, persistence, and formulation challenges as well as profound test for non-target effects. Advancements in extraction techniques and biotechnological innovations may improve the efficacy and stability of these plant- and microbe-derived antifungal agents. However, their development raises important considerations. First, although originating from biological sources, once concentrated or formulated these extracts essentially function as chemical compounds rather than classical biocontrol agents, which has implications for regulation, environmental risk assessment, and grower perception. Second, potential non-target impacts on humans, animals, beneficial microbes, and the environment require thorough toxicological evaluation particularly because these products are applied to edible crops such as potatoes. Finally, research into synergistic interactions, resistance management, formulation optimization, delivery systems (e.g., nanoencapsulation, controlled-release carriers), and long-term field validation is essential to ensure commercial viability and durable disease suppression.

Furthermore, it is crucial for the research community to prioritize optimizing dosage, identifying factors influencing efficacy of biocontrol in both field and storage conditions of potatoes, and refining application strategies for the effective use of biocontrol agents. Biological application methods should also prioritize seed and soil treatment, as they serve as the primary inoculum sources for diseases. Additionally, post-harvest applications should focus on optimizing storage conditions to ensure the biological remains effective at their highest potential to limit the progression of these diseases. Exploitation and utilization of native resistant microbial community, identification and cultivation of resistant potato varieties and marker assisted selection within potato breeding programs could also give promising development in the ecofriendly management initiatives. Thus, in order to fully realize the potential and benefits of sustainable potato farming, a combined disease management program including appropriate good field managing practices in combination with biocontrol and improved postharvest storage strategies is recommended to reduce the disease incidence and its spread.

CRedit authorship contribution statement

Apsara Indhu Gopan: Writing – original draft, Visualization, Conceptualization. **Sabine Ravnskov:** Writing – review & editing, Supervision, Resources, Project administration, Conceptualization. **Jens**

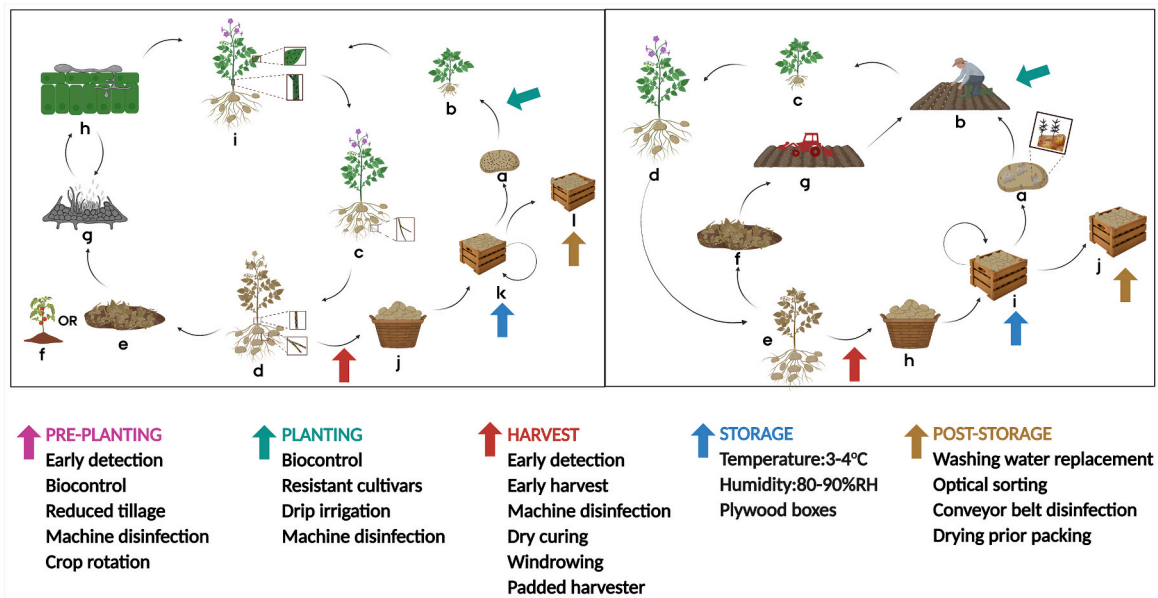


Fig. 5. Proposed combined non-chemical management approach of black dot and silver scurf at various stages of potato production. This figure was created with BioRender (<https://BioRender.com/sby2e0i>).

Grønbech Hansen: Writing – review & editing, Project administration, Funding acquisition. **Isaac Kwesi Abuley:** Writing – review & editing, Supervision, Resources, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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9. Consent for publication

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Ethical approval

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